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TERRITORIAL DISPLAYS OF THE BENGAL FLORICAN[1]

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(*With four text-figures*)

Key words: Bengal florican, bustards, displays, triggers, stimuli

I studied the territorial displays of male Bengal florican *Houbaropsis bengalensis* to understand why their displays are often triggered by calls of unrelated species. Only three of 14 males were within acoustic range of each other. The closest of males were at distances that varied from 0.35 km to 2.25 km (mean 1.2 km, SD 0.67 km, n=14). Males performed two types of territorial displays. The first was by erecting the plumes on the neck and head, and the second territorial display was an exaggerated flight. The flight display was accompanied by auditory signals. Unique to the flight display was a loud clapping sound produced by the wings. There was greater propensity of males within acoustic range of another to display soon after a neighbour displayed. Displays of Bengal floricans were also triggered by calls of other species of birds, chiefly peafowl *Pavo cristatus*, and the jungle crow *Corvus macrorhynchos*. Of 611 display flights recorded, 66% immediately followed such calls. Displays by Bengal floricans were occasionally triggered by other sounds. Calls of the Indian pied hornbill *Anthracoceros malabaricus*, red wattled lapwing *Vanellus indicus*, and on one occasion a gunshot, triggered display.

INTRODUCTION

Territorial displays in the bustards, Otididae, are as spectacular as they are diverse, and can be broadly classified into four categories (Osborne *et al.* 1984). The 'balloon' type display is seen amongst the heaviest members of this group and is the prevalent form of display in the genera *Ardeotis, Neotis* and *Otis* (Mattingley 1929, Cramp and Simmons 1980, Osborne *et al.* 1984, Hellmich 1988; Rahmani 1989). The second is the running type of display, which is seen in the houbara bustard *Chlamydotis undulata* (Mendelssohn *et al.* 1979). The third and fourth categories are both aerial displays and are performed by the smaller members of the bustard group. One of these is a display leap or jump as is seen in the little bustard *Tetrax tetrax* (Schulz 1985) and the lesser florican *Sypheotides indica* (Dharmakumarsinhji 1950, Ridley *et al.* 1985, Sankaran 1991). The other is an aerial display flight and is seen in African bustards such as the black-bellied *Eupodotis melanogaster*, buff crested *E. ruficrista* and black bustards *E. afra* (Osborne *et al.* 1984) and in the Bengal florican (Narayan and Rosalind 1988, Narayan 1990, Sankaran 1991).

Based on their territorial displays, polygynous bustards can be categorized into three types. Species that display on the ground, those that have a jumping display and those whose territorial displays are exaggerated flights. The species that perform jumping displays are the smallest (wing length < 250 mm), those that have flight displays are medium sized (265-350 mm) while those that have ground displays

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are the largest (390-761 mm). The Bengal florican and the black-bellied bustard (342 and 346 mm respectively) appear to be at the size threshold above which all species have only ground displays (Sankaran 1991; source of wing measurements: Cramp and Simmons 1980, Ali and Ripley 1983, Collar *et al.* 1986). These two species are of considerable interest because both have ground displays and aerial displays (this study; Cramp and Simmons 1980).

In the study reported here, I quantitatively describe the territorial displays of male Bengal florican with reference to the kinds of displays performed, frequency of performance by and variation between individuals, temporal distribution of displays and the influence of displays by one male on another. I then examine in detail a fascinating aspect of male Bengal florican behaviour; the phenomenon of calls of unrelated species, for example the peafowl *Pavo cristatus* and the jungle crow *Corvus macrorhynchos,* triggering territorial displays of this species.

Materials and Methods

Study Area: I studied the Bengal florican at four separate grassland sites within the Dudhwa Tiger Reserve (area 815 sq. km), in the northern extremity of Lakhimpur Kheri district of Uttar Pradesh, India (28° 24' and 28° 40' N and 80° 34' and 80° 50' E). The study area lies in the western extremity of the range of the Bengal florican, and differs from areas further east in being relatively drier (cf. Narayan 1990).

The wet alluvial grasslands (*terai*) that comprised my study area were characterised by a few dispersed trees and a distinct mosaic of grass communities. 'High ground' areas were not subject to inundation during the monsoons and were dominated by shorter grass species like *Imperata cylindrica* and *Desmostachya bipinnata.* 'Low ground' areas, which tended to be inundated during the rains were dominated by taller grasses such as *Schlerostachya fusca, Saccharum spontaneum* and *Erianthus munja.* Those areas where water was retained for prolonged periods were characterised by grasses like *Phragmites karka* and *Arundo donax.* The tree cover in the grasslands was sparse; predominantly *Acacia catechu, Dalbergia sissoo* and *Bombax ceiba.* These grasslands bordered dense *Shorea robusta* forests.

The four grassland sites studied varied in area, the sizes being 62, 85, 120 and >250 hectares. The former three had one territorial male each, while the last had three. I named the 5 males studied according to the grassland they occupied. *Kowaghatti, Navalkhad* and *Chapra* (abbreviated accordingly in this paper) were solitary males while *Seethagadaia* East and West were males that were within acoustic range of each other.

Study Animal: The Bengal florican is one of the world's rarest bustards (Osborne *et al.* 1984) and the current world population is estimated at 400 birds (Rahmani *et al.* 1991). It is a large bird (adult males weigh about 1.5 kg), and occupies a monotypic genus in the family Otididae (Osborne *et al.* 1984). This species is promiscuous and exhibits a dispersed lek mating system (Sankaran 1991). In my study area, the breeding season commences in the first week of March and ends at the end of June coinciding with the onset of the monsoon, during which period males occupy territories (briefly described below) that are fiercely defended from other males (Sankaran 1991).

Females did not associate with males, except very briefly. Thus a male performed territorial displays in the absence of females and, in most cases, other males. A distinct pre-copulatory display is performed by males when a female approaches it. Circumstantial evidence showed that parental care is only by the females.

Methods: The study period covered 341 days between 1987 and 1989; from 30 April to 6 June 1987, 22 January to 22 June in 1988, and 15 February to 15 July in 1989.

As males occupied disjunct territories, *machans* (platform) were built on suitable trees in or adjacent to the territories of the males under study. I carried out observations from the *machan* from day break until the bird left the display area. I resumed

observations about 4 hours before sunset and watched the male from when it returned to its display area until it roosted at dusk. Over a period of 10 days, males of each grassland site were observed for the morning and evening on two days.

Observations conformed mainly to the focal animal sampling method (Altmann 1974). The males were observed continuously with a spotting scope and changes in activity (e.g. foraging, standing, preening, display, etc.) were noted to the nearest second.

As peacock calls were the primary triggers of display, the frequency of peacock calls were noted. This followed two methods. Initially I noted down the occurrence of the peacock calls to the nearest second, and its effect on the Bengal florican. Subsequently the number of peacock calls that were heard over every half an hour period were recorded. The timelag between a peacock call and display of a florican was recorded using a stopwatch, the time being measured from the end of the call to the beginning of a display. As peacocks have different calls, the kind of call that triggered display and the presence or absence of triggers each time the Bengal florican performed territorial display were noted. In the case of other sounds which triggered displays (e.g. crow calls), I only noted the type of the trigger.

Results

Territory: The male Bengal florican is territorial, and spacing patterns of territories indicate that the breeding system of this species can be defined as the dispersed lek. The size of male territory varies from 18 to 28 hectares.

Within the territory, a male had a core area from which it displayed; this varied in size between males from 2.1 to 8.4 hectares. Display sites were located in an area of short grass that resulted in males becoming conspicuous as soon as they moved into the 'display area'. All males studied came into their 'display area' about 2.5 to 3 hours before sunset. They roosted at the display sites in the night and left the sites about 3 to 3.5 hours after sunrise. Males generally spent the day in areas of longer grass away from the display sites, but within the territory.

Most males were beyond acoustic or visual range of each other, as the intervening areas were often forested. Of the 14 territorial males that I monitored, 9 were not within acoustic or visual range of another. The distances of the nearest neighbouring males varied between 0.35 km and 2.25 km (mean 1.2 km, SD 0.67 km, n=14). In the grassland which had three territorial males, intra-male distances were between 350 and 400 m.

Types of Display: Males perform two types of territorial displays during the breeding season. The first is a neck fluff display which is achieved by erecting its elongated neck and head plumes, either partly or fully. Partial fluffing of neck feathers resulted in a perceptible thickening of the neck while full fluffing of the neck resulted in the plumes being spread out fully like a fan. The overall mean duration of the neck fluff display was 17 seconds (SD = 32 seconds, n = 679). The mean duration of the full neck fluff was 16 seconds (SD = 32 seconds, n = 482), and that of partial neck fluff was 23 seconds (SD = 16 seconds, n = 197). The full neck fluff display was of a significantly shorter duration than the partial neck fluff display (Mann-Whitney U test, $U = 4179$, $p < 0.002$).

The second territorial display was an aerial one. This flight display consisted of an initial rise to about 3 to 4 metres followed by a descent and then another rise before the male landed in a dive. The mean duration of flight displays was 6.1 seconds (SD =0.59, n = 64). The distance covered by the display flight varied between 15 and 25 metres. The flight display is accompanied by auditory signals. The one unique to the flight display is a loud clapping sound produced by the wings during the first ascent. This lasts about 1-1.2 seconds and consists of between 12 and 15 individual claps. Once the first peak is reached, the bird then begins vocalizing. This is the 'chik' call, but is not unique to the flight display as it is made during regular flight and threat displays as well. Between 4 and 6 individual 'chik' calls are made during each display flight (mean = 5.49, SD = 0.56, n = 33). About 1 'chik' call is made for every 1.1 seconds of display flight.

Nine percent of flight display can be termed as 'extended flight displays' and vary from the normal in that after the first ascent and descent, the male carried on flying and then landed in a display dive (i.e. the second ascent and descent). Or, the display began in the typical manner but did not end in a display dive, or the male began flying normally but landed in a display dive. The average duration of the extended flight display was 16.5 seconds (SD = 7.4, n = 8). Males differed in the frequency of extended flight displays. In two males over 16% of display flights were extended flight displays compared to less than 4% in three others.

The neck fluff display did not always culminate in a flight display. For instance, of 420 territorial displays (both neck fluff and flight) observed in three males, 174 (41%) were neck fluff displays that did not result in the flight display. However, the flight display is preceded by the neck fluff display, the duration of which was variable. The duration of neck fluffing was significantly lower when the fluffing culminated in the flight display than when it did not ($t = -3.406$, $p < 0.001$).

Intensity in territorial display varied. The most passive form was a male advertising its presence by standing in an area of short grass, or on a small mound of sand within its territory and thus becoming very conspicuous. Among active territorial advertisements, the partial neck fluff display was more passive than the full neck fluff display, during which the males were visibly more excited. The most active territorial display was the flight display and it was often a culmination of a series of partial or full neck fluff displays.

Display Periods: Territorial displays are clustered around sunrise and sunset (Fig. 1 a, b). 70% of morning displays occurred within 85 minutes of daybreak and 70% of evening display occurred within 50 minutes to sunset. A peak in number of displays occurred at about 20 minutes after sunrise and 20 minutes before sunset. Only one male out of the five studied showed a preference to display in the mornings (Mann-Whitney U test, $p < 0.01$), the others had no such preference ($p > 0.1$).

The number of display flights performed by males in a display period were few. For almost 25% of observed display periods, males in spite of being present within their territory did not perform flight displays (Table 1). For 80% of display periods, males performed 5 or less flight displays. On an average, males performed between 2.2 and 7.4 display flights per display period (Table 2).

Variation in display rates within the breeding season: The display rates varied considerably between days and even between the morning and evening of a day (Fig. 2 a, b, c). Correspondingly the display rates did not show any consistency between males.

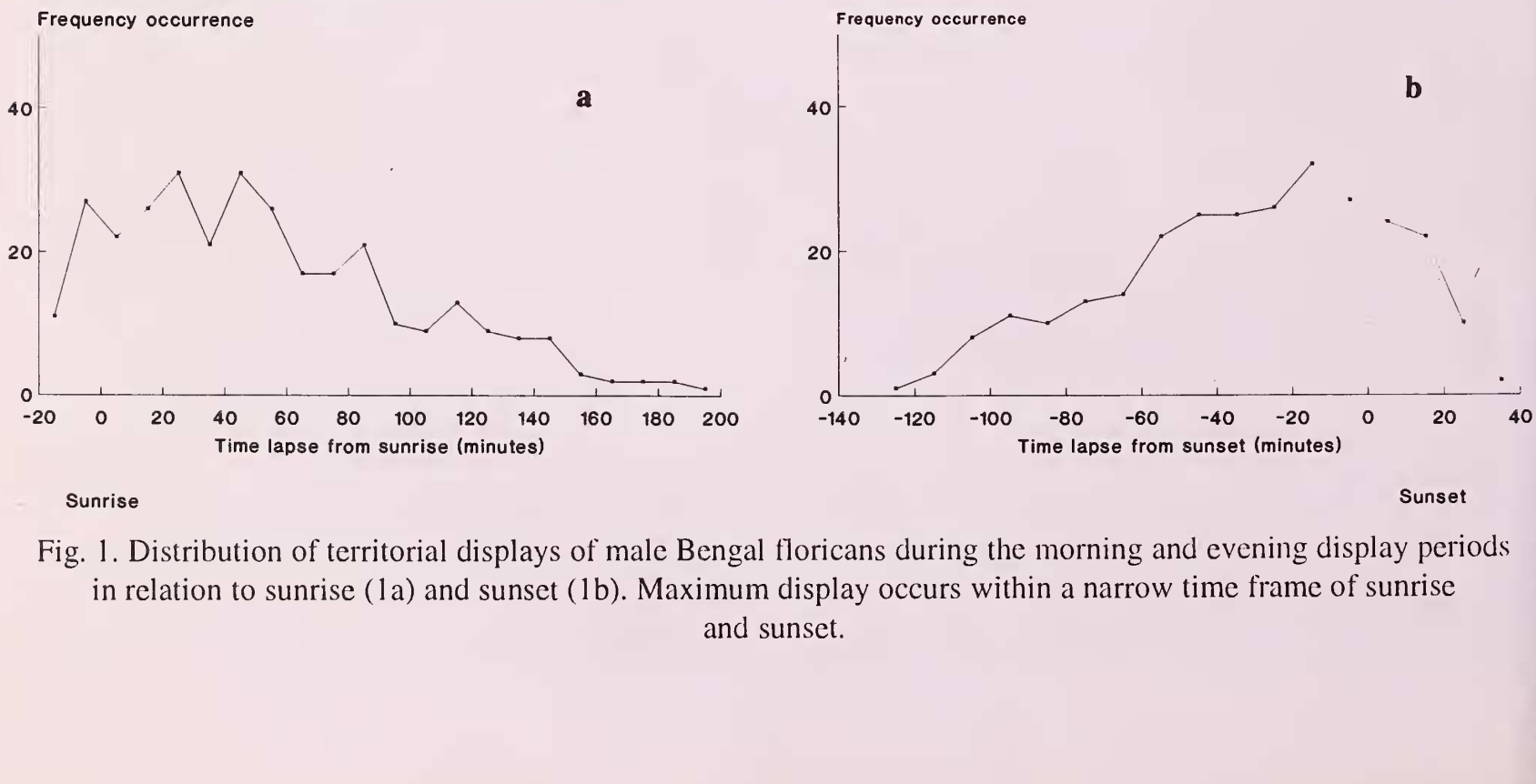


Fig. 1. Distribution of territorial displays of male Bengal floricans during the morning and evening display periods in relation to sunrise (1a) and sunset (1b). Maximum display occurs within a narrow time frame of sunrise and sunset.

TABLE 1

THE NUMBER OF DISPLAY FLIGHTS PERFORMED BY FIVE MALE BENGAL FLORICANS IN A DISPLAY PERIOD. THE FREQUENCY TABLE SHOWS THE NUMBER OF TIMES EACH MALE WAS OBSERVED TO PERFORM 0 TO >9 FLIGHT DISPLAYS DURING A DISPLAY PERIOD. DATA IS FROM 206 DISPLAY PERIODS (BOTH MORNING AND EVENING). (SEE. E., SEE. W., KOW., NAV. & CHAPRA ARE THE IDENTITY OF 5 TERRITORIES

	No. of flight displays performed during a display period											
	0	1	2	3	4	5	6	7	8	9	>9	n.D.P.
See. E.	0	2	1	0	1	0	2	1	2	2	5	16
See. W.	3	1	1	1	4	1	1	2	1	1	0	16
Kow.	12	15	12	11	9	7	4	0	1	1	1	73
Nav.	21	12	9	5	3	7	1	1	1	0	3	63
Chapra	14	8	4	4	0	3	1	2	1	1	0	38
Totals	50	38	27	21	17	18	9	6	6	5	9	206
%	24.3	18.5	13.1	10.2	8.3	8.7	4.4	2.9	2.9	2.4	4.4	

TABLE 2

COMPARISON OF NUMBER OF DISPLAYS PERFORMED PER DISPLAY PERIOD BY FIVE MALES USING MANN-WHITNEY U TEST

	See. E.		See.W.		Kow.		Nav.		Chapra	
			U	p	U	p	U	p	U	p
See. E.			195.5	0.01	171.5	0.01	125.5	0.06	218.5	0.001
See. W.					125.0	0.59	83.0	0.80	169.0	0.12
Kow.							1816.5	0.06	1097	0.07
Nav.									1199.0	0.84
Mean	7.4		4.0		2.8		2.3		2.2	
SD	3.8		2.8		2.5		2.8		2.6	
n D.P.	16		16		73		62		39	

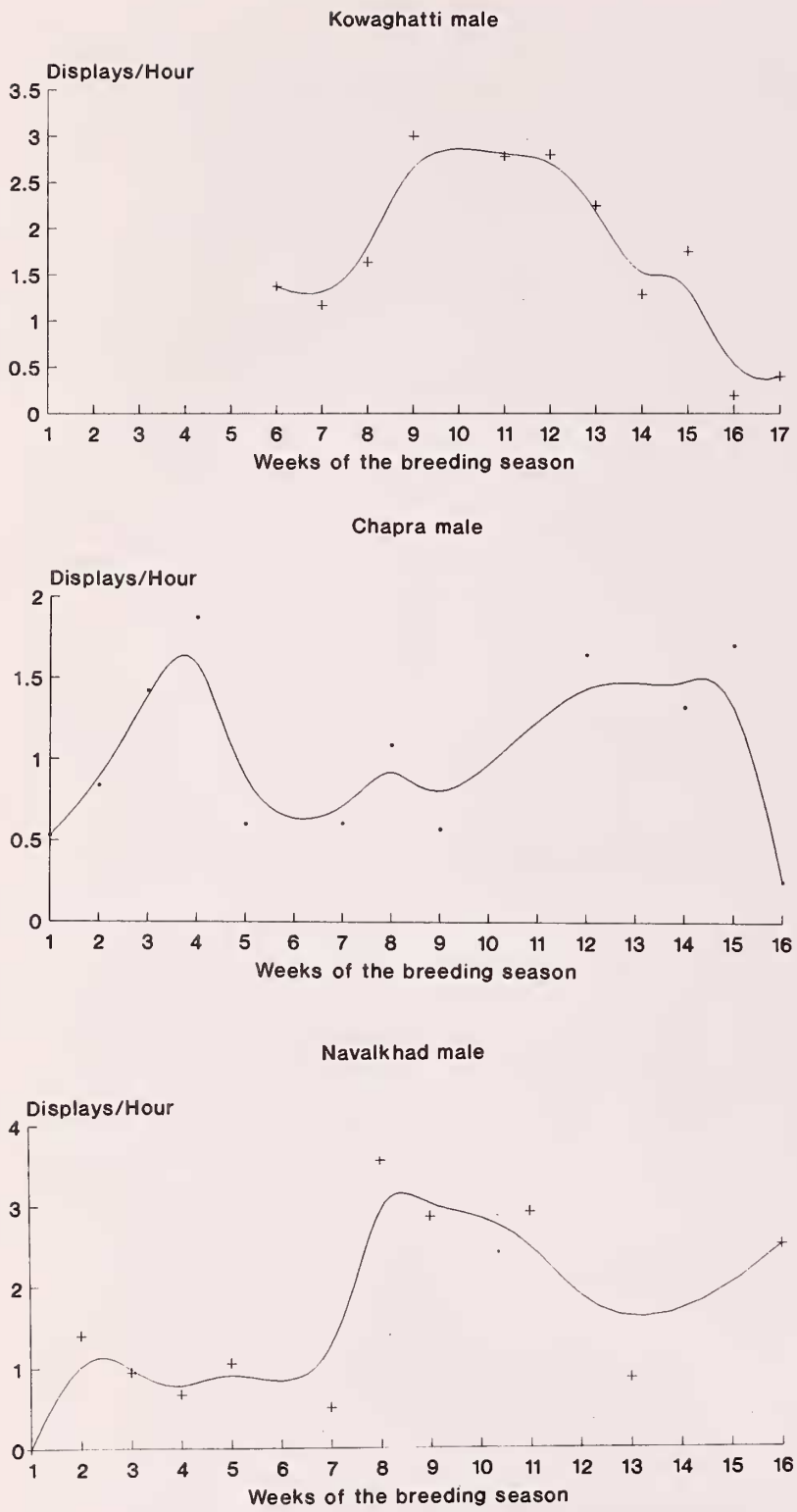
TABLE 3

DIFFERENCES (BY T TEST) IN THE MEAN DURATION OF THE NECK FLUFF DISPLAY THAT WERE TRIGGERED BY CALLS (PEACOCK AND CROWS) AND NOT TRIGGERED BY CALLS

	Neck Fluff followed by flight display					Neck Fluff not followed by flight display				
	WPC		WNT		WCC	WPC		WNT		WCC
	T	P	T	P		T	P	T	P	
WCC	2.433	0.021	-1.214	0.240		1.668	0.103	0.681	0.501	
WNT	2.387	0.028				2.539	0.017			
Mean	0.153		0.263		0.180	0.264		0.448		0.580
SD	0.259		0.241		0.130	0.192		0.301		1.255

Key : WPC = With peacock calls; WCC = With crow calls; WNT = Without sound triggers

A sound was said to have triggered a display when there was no time lag between the end of the sound and the commencement of display, that is, the sound began slightly before males responded by displaying.



Curve-least square fit; Data from 1989

Fig. 2. Variation in weekly display rates of three male Bengal floricans through the breeding season.

Variations in display rates between males: I tested display rates to see whether variations existed between males and whether two males which were within acoustic range of each other had greater display rates than solitary males. Though the display rates of the males that were within acoustic range were higher than the solitary males (Table 2), only one of these males (See. E.) had significantly higher display rate than the others. Even between solitary males differences existed in the number of displays performed during a display period.

Stimuli and Triggers: Of the 14 identified territorial males in the study area, only 3 males were within acoustic range of each other. There was a greater propensity of these three males to display soon after a neighbour displayed. On some occasions (7%) one male responded to another by displaying immediately, that is both were in the air together. More often (27%), males displayed a short time (within 2 minutes) after a rival displayed (Fig. 3).

Displays of Bengal floricans were often triggered by the calls of other species of birds, chiefly peafowl, and to a lesser extent the jungle crow. A sound was said to have triggered a display when there was no time lag between the end of the sound and the commencement of display (0 seconds), that is, the sound began slightly before males responded by displaying.

Of the 611 display flights recorded, 66% immediately followed such calls. Of these, 72% followed peacock calls and 28% followed crow calls.

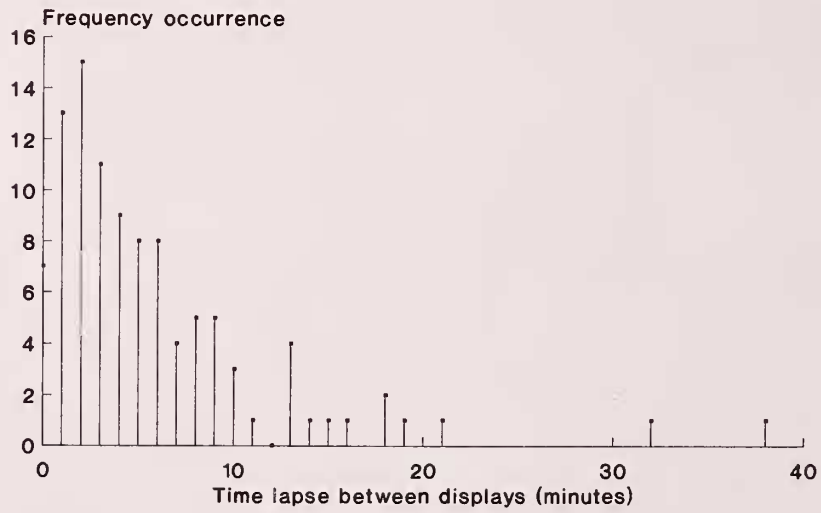


Fig. 3. Time lapse between flight displays of three male Bengal floricans which were within acoustic and visual range of each other. Males tend to display within a narrow time frame of another male's display.

59% of instances of neck fluffing was not followed by flight display (n = 509) were triggered by calls. 87% of these were triggered by peacock calls and 13% by crow calls. Displays by Bengal floricans were occasionally triggered by other sounds. Calls of the Indian pied hornbill *Anthracoceros malabaricus,* red wattled lapwing *Vanellus indicus,* and on one occasion a gunshot, triggered either neck fluffing or flight display.

I measured time lapse between peacock calls and Bengal florican displays. Of the 196 instances when time lapse could be measured between the end of a peacock call and the commencement of a display, 82% of displays occurred while the peacock was calling (Fig. 4). A uniform distribution of displays at all other intervals show that there was no lag effect of peacock calls on the Bengal florican's display, and that the call had an effect for that instance only.

As both peacock calls and Bengal florican displays occur at greatest intensity in a narrow time range, that is, at sunrise or sunset, it was possible that both occurred at identical moments purely due to chance. On testing the data I found that Bengal florican displays had a significantly higher probability of following peacock calls than that expected purely by chance (chi square 277.5, DF 1, $p < 0.0001$).

I examined the effect of the presence and absence of sound triggers on the duration of neck fluff display. I expected to see two patterns. Firstly, if there was a difference in the degree of trigger effect between calls, I expected that the duration of neck fluff display culminating in flight display would be least in those displays triggered by peacock calls. Secondly, because triggers have an instantaneous effect on display, I expected that the duration of neck fluffing will be longest when the neck fluff display occurs independently of triggers.

Correspondingly, I divided neck fluff displays into two: (a) when the flight display followed, and (b) when the flight display did not follow. As expected, when displays were triggered by peacock calls, the duration of neck fluff was significantly lower than in those displays which were triggered

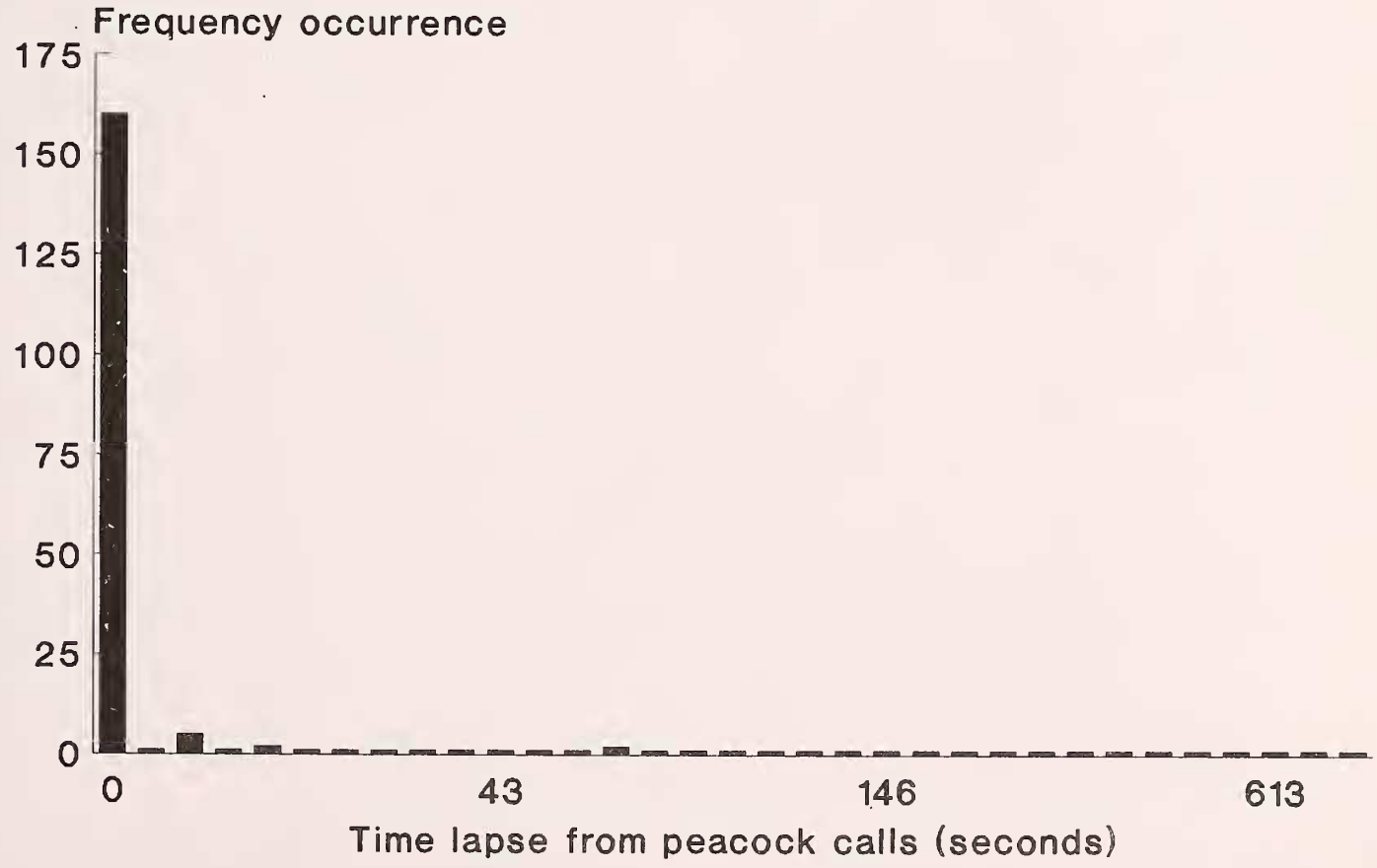


Fig. 4. The time lapse between peacock calls and the displays of male Bengal florican. Display at 0 seconds indicates that both display and calls occurred at the same instant. The effect of a trigger releasing display is instantaneous, and apparently does not have a delayed (or lag) effect.

by crow calls or which occurred independent of triggers (Table 3). However, though the mean duration of neck fluff was greater when flight display occurred independently of triggers than when triggered by crow calls, the data did not vary significantly.

Similarly, when not followed by display flight, neck fluff displays triggered by peacock calls had significantly shorter duration than neck fluffing without triggers. The duration of neck fluffing triggered by crow calls did not vary statistically from the other two, though the mean value was the highest (Table 3).

To see whether there was any variation in trigger effect in the loudness of peacock calls, I ranked calls as loud, medium or faint. Loud calls were those which were assessed to have been emitted within 150 m of the male florican, medium 150 - 300 m, and faint calls were over 300 m away. Of all peacock calls that acted as triggers, 49.48% were loud, 32.47% were medium, and 18.04% were faint.

Peacock calls are varied, but the three most common are the '*Mayaw-Mayaw*', the '*Kia-Kia*' and the '*Kok-Kok*' and variations of these calls. Of these the last is almost purely an alarm call while the former two are contact and/or territorial calls. Displays of the Bengal florican are mainly triggered by the '*Mayaw-Mayaw*' calls. Only on three occasions did the '*Kia-Kia*' call trigger displays, two of which were flight displays, and one was neck fluffing. Twice, variations of these calls triggered off flight displays.

Discussions

There are two main features of the territorial displays of the Bengal florican that need emphasis. (1) The low number of displays that males perform during a display period and the lack of a distinct peak in display during the breeding season and (2) the existence of triggers and stimuli in territorial displays.

Territorial displays are signals that pass on information both to rival males and to females. Displays however are of many forms, and include at one extreme specifically evolved advertisements and at the other by simply being conspicuous within its territory by for example standing in a prominent position so that other individuals can easily see it. The form the display takes will determine the distance over which the message is signalled. Amongst bustards, both ground and aerial displays are seen, larger bustards have ground displays whose effective signalling distance is enhanced by males displaying from higher ground (e.g. Rahmani 1989). Small bustards have jumping displays because the effectivity of the signal is enhanced by the male rising above the vegetation.

However, a territorial signal will be effective only if it is performed frequently enough. Male lesser floricans display jump as many as 500 times a day (Sankaran 1991) and male great Indian bustards may perform their balloon displays for as long as an hour or more continuously (Rahmani 1989). For both these species, display is the prominent activity during the breeding season. In contrast, male Bengal florican perform less than 4 or 5 flight displays during a display period.

The frequency of aerial displays will be limited by, among others, body size. Adult male Bengal florican are medium sized bustard that weigh about 1.5 kg. I suggest that due to energy limitations brought about by size, frequent displays (like, for example, the lesser florican) cannot be performed. However, for territorial displays to be optimally effective, the message must be signalled frequently, or over a longer duration of time (as is the case with the lesser florican and great Indian bustard). The Bengal florican has two forms of displays. Aerial displays, in its grassland habitat have the function of signalling over longer distances. The ground displays, on the other hand have signalling value over shorter distances. I suggest that the low frequency of flight displays that signal over longer distances are compensated by advertisements that are effective over shorter distances.

The lack of distinct peaks in the display rate over the breeding season can be best explained by the nesting patterns in hens. Nesting occurs through every month of the breeding season (Baker 1921). This is an expected response as nesting habitat and

food are abundantly available for most of the breeding season (Sankaran 1991). If receptivity in females is not concentrated to specific parts of the breeding season, and females solicit males throughout, then males too should not have distinct peaks in display rates.

Males occasionally display immediately on hearing a rival display, but more often males display a short while after a rival displays. I believe that this pattern is an expected one. A display signals a message, and in territorial displays it probably signals strength or ability to retain its territory. So a male should listen to or watch a rival male's display in order to assess the other before it responds. The few occasions when the males responded immediately to a rival's display by displaying can they be easily attributed to higher levels of pugnacity at that moment.

The calls of unrelated species acting as releasers of Bengal florican's displays is less easily explained. To explain why Bengal floricans display to calls of other species, I use a proximate approach rather than an ultimate one. The essential problem of using an ultimate approach is that possible explanations that were examined, did not account for the immediate response by the males to calls of unrelated species. I believe that the observed behavioural pattern can be explained by classical ethology from which period experimental demonstrations of complex behavioural patterns being triggered by a variety of objects exist (Gould 1982). Though this approach has lost popularity in recent times (McFarland 1985), the concept of the 'Fixed Action Pattern' and 'Sign Stimuli' has stood up to examination and shows no real sign of 'diminished usefulness' (Thorpe 1979). I believe that this approach is all the more valid in this case because, as a rule, territorial or courtship displays are innate and are not learned.

The sounds which trigger Bengal florican's territorial displays are diverse and include calls of peafowl, jungle crow, Indian pied hornbill, red wattled lapwing, swamp partridge and gunshots. Displays can be triggered by humans mimicking peacocks (Narayan and Rosalind 1988). It was thus apparent that it was not a call *per se* but sound which triggered displays. I suggest that this is a case of sound acting as a sign stimuli to release displays, in much the same pattern as has been demonstrated by Tinbergen (1951, 1972) for such diverse life forms such as butterflies, fish and birds.

I am unsure as to how this fixation of sounds triggering displays came to exist in the Bengal florican. One possible explanation lies in the observation of males being stimulated (sometimes immediately) to display on hearing the acoustic signal (wing clap) of the flight display of a rival male, and this perhaps leading to sound being fixed as a trigger in floricans.

The propensity of peacock calls triggering displays needs further perusal. If sound triggers display, then the loudest sounds are those that should elicit the most reactions ('super normal sign stimuli'; Tinbergen 1951, 1972). Peacock calls are amongst the loudest sounds in the Bengal florican's habitat and are therefore essentially 'super normal sign stimuli'. In the absence of loud calls, other sounds should release display as indeed indicated by the trends in data collected. This is also corroborated in the duration of neck fluff being significantly lower when triggered by peacock calls, thus indicating a stronger trigger effect, as is to be expected of the functioning of a 'super normal sign stimuli' (Tinbergen 1951, 1972). Though the existence of sign stimuli releasing fixed action patterns has several advantages, occasionally responses to cues which are obviously inappropriate exist, which with a slight increase of 'specificity in filtering mechanisms', might have been avoided (Gould 1982). This is important in context to the Bengal florican, because the sounds that trigger a complex breeding activity, territorial display, are cues that are irrelevant to its breeding.

Another question of interest is why has such behaviour evolved in this species, while in others, which also have acoustic components to display, such trigger patterns are not apparent?

A striking feature of Bengal florican attraction displays is their sporadicity. In 90% of observed

display periods, males performed 7 or less flight displays; as each display flight has a duration of about 6.1 seconds, the time over which the male was actually displaying is minuscule. Thus display is not an activity that occupies time, but exists as individual acts. This is in striking contrast to other species of bustard, e.g. lesser florican where males can display at rates up to 2 or 3 jumps per minute for an hour or more (Ridley *et al.* 1985, Sankaran 1991), or the great Indian bustard, in which display also occupies considerable periods of time (Rahmani 1989).

I suggest that the existence of triggers in displays in the Bengal florican has arisen because of the sporadicity of its displays. In species where display occurs continuously over periods of time, a stimulus can elicit a bout of display but not each display act, as these are performed too frequently. In the Bengal florican, however, sporadicity of display has resulted in each display act being a single independent unit, i.e. one display flight is not immediately followed by another (as in the lesser florican) but after a significant time lag. Thus the fixation of unrelated triggers or the use of 'simple sign stimuli' to release behaviour sequences appears to be a function of the sporadicity or the rarity of the performance of an act.

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